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ZOÖLOGICAL BULLETIN.

THE AMPULLAE OF LORENZINI OF THE SELACHII.

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I SHALL give in this paper an abstract of some of my results obtained from work on the smooth dogfish (*Galeus canis*, Mitchill), reserving the plates and a fuller description of the lateral-line system, ampullary organs, and Savi's vesicles (of Torpedo) for a more extended paper.

The most casual observation of any of the elasmobranch fishes shows the presence of a large number of pores opening upon the surface. When the skin is pressed a thick, gelatinous, transparent substance is seen to ooze from them, which on mixing with the water covers the surface of the fish with slime. A closer observation and a careful dissection is necessary to establish the fact that these pores must be classed in two distinct groups : to the one group belong the pores of the lateral-line system, and to the other the pores of the ampullary tubes. It is well-nigh impossible in many genera to distinguish superficially the one class of openings from the other.

In tracing the course of the lateral-line canals I have employed the following method. The canals were cleared from their mucous contents by forcing ether through them by means of a syringe and fine canula. When the ether had made its way through all the canals and tubules, an injection mass com-

posed of thick celloidin colored with Prussian blue was used until it appeared at all the pores belonging to this system. The specimen was then put into 20% nitric acid and left for one to three days, until the skin and tissues were softened enough to be easily removed with needle and forceps. A careful dissection left a deep blue cast of the canals with their finest ramifying tubules. Maceration is stopped and the preparation kept indefinitely in a 2% formalin solution. The course of the ampullary canals was readily followed by probing with black bristles.

Since 20% nitric acid softens bone, muscle, and connective tissue, at the same time hardening more or less the nerve tissue, specimens which have been thus macerated for a day or two furnish favorable material for tracing nerve trunks and fibers to their finest ramifications.

For general histology Hermann's fluid and corrosive sublimate have proved the best fixing agents. Iron haematoxylin, with orange G as a counter stain, has given very satisfactory histological results.

Method employed in using Methylene Blue. — After considerable experimentation I have come to adopt the following as a method of procedure for the successful application of methylene blue to selachian material. The head of a live dogfish is severed from the trunk, the snout cut open, and a solution of methylene blue injected with a hypodermic syringe into the gelatinous tissue in which the ampullae are imbedded. I have obtained equally good results with $1\frac{1}{2}\%$, 1%, $\frac{1}{10}\%$, $\frac{1}{20}\%$ solution of the blue, but have found the $\frac{1}{10}\%$ the most convenient. After the stain has been allowed to act for an hour and a half, a small clump of the ampullae is removed to a slide and teased out so that each ampulla is isolated and thus exposed to the air. The slide is then examined under a low power.

One of the most important factors in securing a successful stain is that of exposure of the tissue in the air. I have often found on looking over an apparently worthless series of ampullae a second time that the fibers have become well stained, this result being due apparently to the few moments of further

exposure. Indeed, by careful watching one can see the stain creep along the nerve trunks and the fibrillae out to the finest ramifications. If the stain has worked successfully the fine fibrillae will stand out as sharp blue lines all over the surface of the ampulla, all the rest of the tissue remaining colorless.

Fixation of the blue is accomplished by removing the ampullae into a solution of ammonium molybdate. I have modified somewhat Bethe's original formula (*Archiv f. mik. Anat.*, 1895, Bd. xliv, pp. 579–588) in substituting osmic acid for hydrochloric, using the following solution:

Ammonium molybdate . . .	1 gr.
Distilled water	10 cc.
Peroxide of hydrogen . . .	1 cc.
Osmic acid, 1%	1 drop.

This mixture seems to fix the blue stain more perfectly than any other I have tried, and has two additional advantages: first, that of differentiating the medullary sheaths of the nerves; secondly, that of better histological preservation of the tissue. I have not found the use of ice, recommended by Bethe, necessary for the preservation of the blue.

After remaining in the fixing fluid for one to two hours the ampullae are washed in water for ten minutes, then hurried through the grades of alcohol, cleared in toluol and imbedded in paraffin. Since these organs are so small (about 1 mm. in diameter), twenty minutes in each fluid and an hour in paraffin I find to be sufficient. An injection of the blue may therefore be made at 10 A.M. and by 5 P.M. one may cut a series of sections. The histological character of the cells after such treatment is not very perfect, but the nerve fibers with their branches stand out very sharply defined.

Since alum carmine does not impair the blue it has given the best results as a nuclear stain for sections.

Many facts of nerve relations can best be determined by treating the tissue in the following way. Ampullae well stained with the methylene blue are fixed in ammonium picrate, and frozen by the use of carbon dioxide on a freezing microtome attachment. Freehand sections are cut with a razor

and mounted in a mixture of dilute glycerine and ammonium picrate. If the slide is sealed with asphaltum the preparation may be kept for several weeks. The sections are best studied at once, however, as the blue tends either to fade or to become granular, the fibrillae losing their continuous appearance.

My experience with methylene blue as applied to selachian material has led me to the following conclusions: (1) The tissue must be alive when the blue is applied. I have never had a successful impregnation unless the head is removed from a live animal and injected at once. (2) The strength of solution seems unimportant, since I have obtained a good stain with such extremes as 1½% and $\frac{1}{20}$%. (3) The most important facts to be learned to obtain success with a given tissue are, first, the time which the stain should act on the tissue before exposure to the air, and second, how long an exposure is necessary. The time limits which give success with dogfish do not give good results with skates. (4) The best results are obtained from ampullae which seem scarcely tinged with the blue. When the tissue is deeply stained one finds on examination with the low power of the microscope that the stain is located in the cells, not in the fibers. (5) It is impossible to carry the methylene blue through the paraffin bath unless the tissue is completely dehydrated, hence the importance of securing genuine absolute alcohol. (6) I have been unable to preserve the stain in alcohol or in the clearing oils for any length of time. I have cut paraffin blocks, however, a year after the objects were imbedded, and the blue seems perfectly preserved. This seems the surest means of preservation of the stained tissue till one is ready to use it. Sections mounted in balsam or dammar in August, 1895, have not lost a bit of their clearness.

Groups of Ampullae. — Following Ewart's nomenclature I shall designate the groups of ampullae according to their innervation as supra-orbital, buccal, hyoid, and mandibular. In Galeus it seems impossible to distinguish the supra-orbital and buccal.

In order to determine the number in each group the ampullae were carefully dissected out and counted in two speci-

mens, one a female 1.07 m. long, the other a pup 26 cm. long. The following are the results of my computation:

	IN ADULT.	IN PUP.
In supra-orbital-buccal groups . .	1029	860
In right hyoid group	270	273
In left hyoid group	245	287
In right mandibular group . . .	25	19
In left mandibular group . . .	26	19
Totals . . .	1595	1458

On comparing the two columns of figures it will be seen that the number of ampullae probably does not increase after the birth of the fish, as in some groups the number is larger in the pup. The difference in the total number is probably due to individual variation.

The ampullae are imbedded in a matrix of clear gelatinous tissue, through which run the nerves supplying these organs. The whole mass is surrounded by fibrous connective tissue which is pierced by the tubes as they run out from the ampullae.

Gross Anatomy of an Ampulla. — At its inner end each ampullary tube from the surface opens into one of the so-called ampullae of Lorenzini (Fig. 1, *a.*). Viewed from the side an ampulla is seen to be a sac more or less spherical in form, with slight outpocketings (Fig. 1, *a.pkt.*) which vary in number from eight to twelve. If one looks at the proximal end of the ampulla, the pockets are clearly seen as a circle of protuberances. The internal structure is best made out when the ampulla is sectioned transversely in a plane just above its largest diameter. Looking into the organ one sees the out-pocketings noticed on the outside, while partitions also appear running from the divisions between these pockets

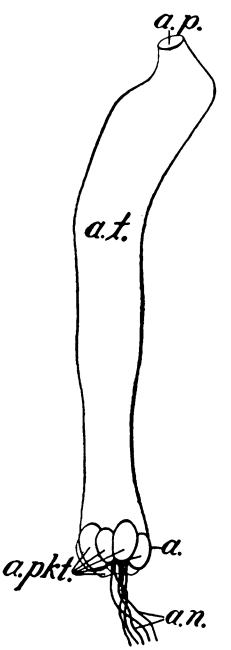

FIG. 1. — Outline drawing of tube and ampulla: *a.*, ampulla; *a.n.*, ampulla nerve; *a.p.*, ampulla surface pore; *a.pkt.*, ampulla pocket; *a.t.*, ampulla tube. × 12.

toward the center. The lumen at the base of the ampulla is thus divided into the above-mentioned eight to twelve compartments (Fig. 3, *a.pkt*). A columnar structure (Fig. 2, *a.c.*) to which the partitions run, is formed in the center of the ampulla. To this structure Boll has applied the name "centrum." The centrum increases in diameter considerably above, so as to form a slightly concave, plate-like cap (Fig. 2, *a.c.c.*), which covers over a portion of the compartments beneath. In longitudinal sections of the ampulla taken through a partition (Fig. 2), it is seen that the edge of the partition curves upward as it passes from the centrum to unite with the outer wall.

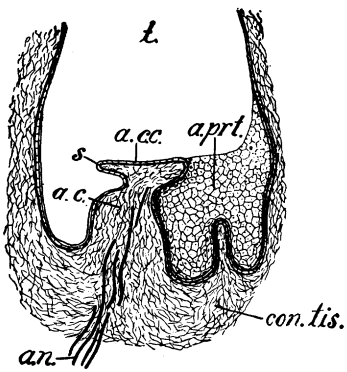

FIG. 2. — Longitudinal section of ampulla through centrum, plane of section passing through an ampullary pocket on the left side of the figure and through a partition wall on the right: *a c.*, ampulla centrum; *a c.c.*, ampulla centrum cap; *a.n.*, ampulla nerve; *a.prt.*, ampulla partition; *con tis.*, connective tissue; *t.*, ampulla tube. × 51.

The average diameters of the ampullae of a dogfish 1.02 m. long are as follows:

In the supra-orbital-buccal groups . .	$\frac{9}{10}$ mm.
In the hyoid groups	$\frac{7}{10}$ mm.
In the mandibular groups . . .	$\frac{3}{10}$ mm.

Histology of Tube and Ampulla. — In histological structure the tubes are comparatively simple. They are lined with a single thin layer of epithelial cells. In surface view the outlines of the cells, most clearly made out from a silver nitrate impregnation, are seen to be polygonal. The oval nuclei have a diameter about one-third that of the cells. In cross sections (Fig. 4, *t.c.*) the nuclei appear as thin ellipsoid bodies, staining deeply. Nucleoli are visible. The shape of the cell body is more difficult to determine, since the nucleus occupies so large a part of its thickness. But after using several methods of fixing and staining I am confident the section of the cell is spindle-shaped, the thickness decreasing from the center toward the periphery, until at the point where two cells are

contiguous the cytoplasm appears like a single thin line (Fig. 4, *z.*). Outside this layer of cells is a sheath of connective tissue of varying thickness constituting the larger portion of the wall of the tube (Fig. 4, *con. tis.*).

The histology of the ampulla is best studied in a longitudinal section. Two regions, distinguished by the character of the lining cells, are to be recognized. First, the centrum cap is covered on its upper surface with a single layer of cells usually

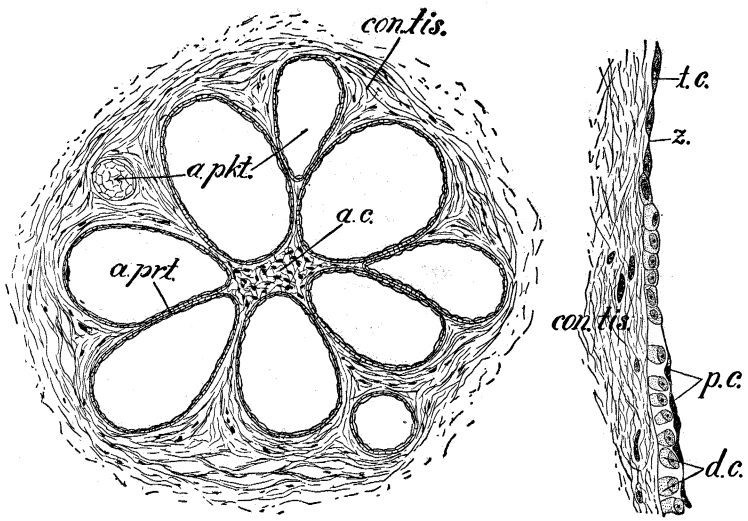

FIG. 3. — Cross section of ampulla below plane of centrum cap: *a.c.*, ampulla centrum; *a.pkt.*, ampulla pocket; *a.prt.*, ampulla partition; *con.tis.*, connective tissue. × 63.

FIG. 4. — Longitudinal section of upper portion of ampullary pocket and of tube: *con.tis.*, connective tissue; *d.c.*, deeper layer of cells; *p.c.*, peripheral layer of cells; *t.c.*, tube cells; *z.*, point where two cells of tube wall meet. × 465.

almost cubical in shape (Fig. 5, *c.c.*[1]). The oval nuclei are large. In many sections the cytoplasm toward the lumen of the tube pushes out into a blunt process, the line of cells in the section then having the appearance of irregularly placed saw-teeth. This same single layer of cells covers the under side of the centrum cap (Fig. 5, *c.c.*[3]), where the latter arches over the ampullary compartments. At the edge of the cap the cells become more elongated, often spindle-shaped (Fig. 5, *c.c.*[2]). The partition walls near the centrum are likewise cov-

ered on either side with a single layer of cells. In the second region, *viz.*, that of the walls of the pockets themselves, two layers of cells are always found. The peripheral layer, that is, the thin sheet of cells next the lumen (Figs. 4, 5, *p.c.*), has an appearance almost exactly like that of the lining of the tube. The cells are flattened, each being almost entirely filled by an ellipsoid nucleus. Nucleoli are prominent. Beneath this thin epithelial layer is a second layer composed of short cylindrical cells (Figs. 4, 5, *d.c.*). The nuclei, large and spherical in shape, are situated at the very ends of the cells, next the peripheral layer. The nuclei of the two layers can be easily distinguished, not only by their difference in form, but also by a difference in their reaction to stains, that is, those cells next the lumen take a deeper stain.

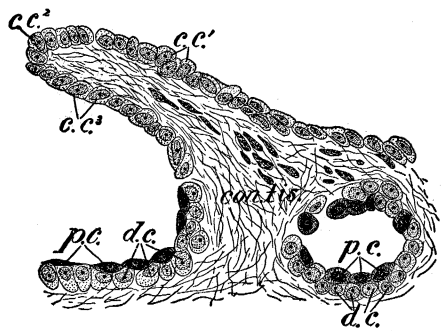

FIG. 5. — Region of Fig. 2 marked *s.*: *c.c.* 1-3, centrum cell; *con.tis.*, connective tissue; *d.c.*, deeper layer of cells; *p.c.*, peripheral layer of cells. × 465.

Innervation of Ampulla. — Five to ten nerve fibers run to each ampulla (Fig. 1, *a.n.*). I have never seen the fibers branch or unite with one another after leaving the nerve trunks. In branching, the nerve trunks simply give off some of their component fibers.

In studying the course of the nerves in the ampulla I have employed the methylene blue method altogether, and this method has given very satisfactory results. When the blue is fixed in the ammonium molybdate with the addition of osmic acid, a longitudinal section in a median plane shows that a medullary sheath encloses the axis cylinder of the nerve along its course up the centrum till just beneath the centrum cap, where it disappears rather abruptly (Fig. 6, *n.m.sh.*). In freshly stained specimens, or where the stain is fixed without the osmic acid, the blue-stained nuclei of Schwann's sheath are distinctly visible.

After the loss of the medullary sheath the axis cylinders pass

upward for a short distance, then divide more or less dichotomously, sending out branches at right angles to their former course (Fig. 6, *n.ax.cyl.*). By the interlacing of these axis cylinders a plexus is formed, occupying nearly the whole area of the centrum cap. All the best results of previous workers were obtained by the use of osmic acid. Since this reagent differentiates the medullary sheath only, their observations could be carried only to the point where this sheath disappears. The fibers were then pursuing a perpendicular course, and the assertion was but natural that this course was continued for a

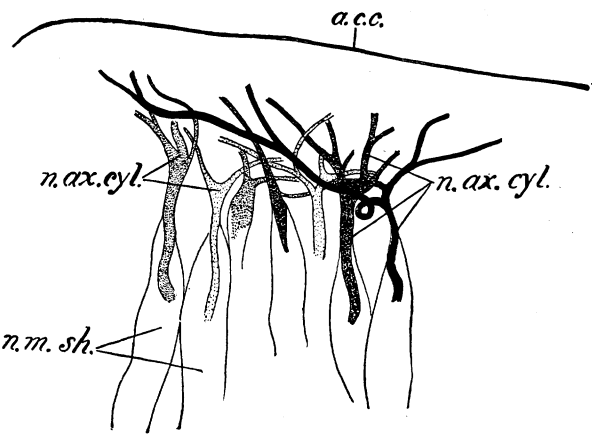

FIG. 6. — Nerve fibers in longitudinal section just below centrum cap : *a.c.c.*, ampulla centrum cap; *n.ax.cyl.*, axis cylinder of nerve ; *n.m.sh.*, medullary sheath of nerve. × 465.

very short distance, the fibers then coming into connection with the cells at the top of the centrum. As we have seen, this is not at all true. From the plexus already described bundles of axis cylinders collect at the periphery of the centrum cap, and pass out into the connective tissue of the partitions which separate the ampullary pockets. Thus far the nerves have, so to speak, avoided all relations of contact or of continuity with cells.

Having passed into the region where the double layer of cells is found, the nerve fibrils begin to divide, sending out branches which play over the bases of the deeper layer of cells (Fig. 8, *n.ax.cyl.*). The manner of giving off branches is interesting. In well-stained specimens (Fig. 7) the larger axis cylinders are

seen under the highest powers of the microscope to be made up of minute fibrillae. For a distance along their course these fibrillae are separated more or less from one another, but at certain points they are gathered tightly together (Fig. 7, *v.*). When branches are given off, the individual fibrillae may be traced continuously from the larger axis cylinders out along the smaller branches (Fig. 7, *n.ax.cyl.*). On these finer branches is seen the same appearance of collecting and loosening out of fibrillae as has been described above. Such a fact

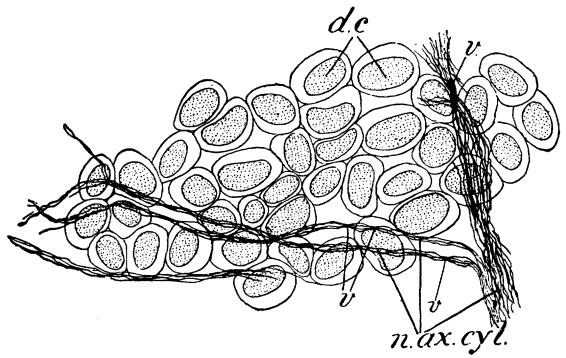

FIG. 7. — Method of branching of axis cylinders of nerves: *d.c.*, deeper layer of cells; *n.ax.cyl.*, axis cylinder of nerve; *v.*, points along course of axis cylinders where the nerve fibrillae are gathered closely together. × $\frac{1}{12}$ oil immers. 2 in. occular.

suggests that the finest individual nerve fibril may be continuous from its peripheral termination back through the bundle of fibers in which it has come, to its ganglion cell near or in the brain.

Along the course of the finest fibrillae little thickenings are seen just at the base of the cells of the deeper layer (Figs. 8, 9, *n.k.*). Thus far I have never seen any branches running up between the cells. If such branches were present I believe they would be stained as the others are by the methylene blue. The distribution of the nerves as described above has been seen in many series of sections.

In thick sections obtained by freezing and fixing the blue with ammonium picrate the cells are stained yellow, the fibers assuming the purple color characteristic of this treatment. If one examines with very high powers the outer surface of the

ampullary pockets, the nuclei of the thin lining layer of the pockets are clearly seen on deep focusing; at a higher focus the outlines of the cells and nuclei of the deeper layer appear; at a still higher focus the nerve fibrils are sharply differentiated (Fig. 7). Since these nerve fibrils appear at neither of the two first-mentioned optical levels the observations made from sections of the ampullary walls appear to be confirmed, namely, that the nerve fibrils ramify only over the bases of the cells of the deeper layer.

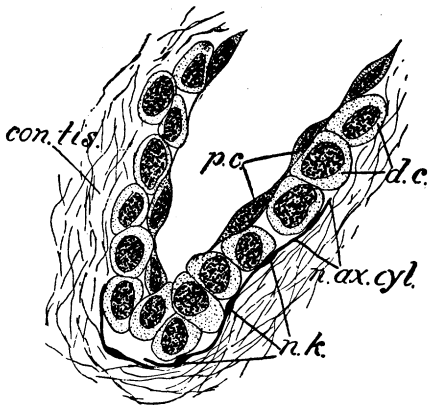

FIG. 8. — Longitudinal section of wall of ampullary pocket: *con.tis.*, connective tissue; *d.c.*, deeper layer of cells; *n.ax.cyl.*, axis cylinder of nerve; *n.k.*, nerve knob; *p.c.*, peripheral layer of cells. × $\frac{1}{12}$ oil immers. 2 in. occular.

In frozen sections prepared as described above, the cells may be isolated from one another by tapping the cover glass. I have seen in several cases a fine, deep-blue fibril running along the surface of the deeper cells and ending

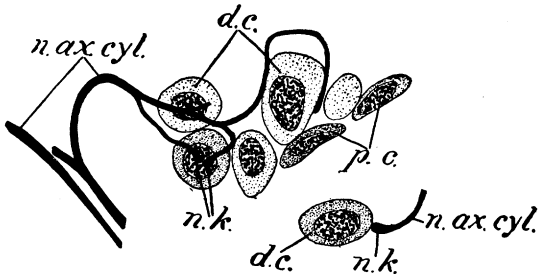

FIG. 9. — Nerve fibrils running over the surface of the deeper layer of cells to end in knobs on the outside: *d.c.*, deeper layer of cells; *n.ax.cyl.*, axis cylinder of nerve; *n.k.*, nerve knob; *p.c.*, peripheral cell. × $\frac{1}{12}$ oil immers. 2 in. occular.

in a slight enlargement (Fig. 9, *n.k.*). These fibers and endings are always *outside the cells*, and it is apparent that the protoplasm of the two structures is not in continuity, since the cells are usually of a yellow color, while the nerve fibrillae are

deeply stained with the blue, the line of separation between the two appearing quite distinct.

To recapitulate the facts of innervation as given by the methylene blue : Five to seven medullated fibers coming from the (seventh pair of) cranial nerves enter each ampulla from below and pass up the centrum. Just beneath the centrum cap the sheath disappears. The axis cylinders, continuing on their course, send out lateral branches, which after division and ramification beneath the centrum cap run out along the partitions to the outer walls of the compartments. Here minute fibrils play over the bases of the deeper layer of cells, ending in slight enlargements on their surfaces. This much of the innervation of an ampulla has been given sharply and clearly by the use of the methylene blue. Since nothing further in the way of nerve structure has been suggested by the method, it seems to me the theories of the function of the ampullary organs must conform to these facts.

Physiology. — Of the theories thus far suggested to explain the function of the ampullae of Lorenzini, but two are supported by anatomical facts: either they are sense organs, or they are glands for the secretion of mucus.

The wealth of nerve supply for these organs almost compels one to believe that they must be sensory in character. This theory was first advanced by Jacobson (**1813**), and in most of the important papers on these organs since that time, including those of Muller ('**51**), Leydig ('**68**), Boll ('**68**), Merkel ('**80**), Ewart ('**92**), the writers have maintained the view that the ampullae were sense organs.

The histological structure of the epithelium lining the pockets does not, however, show the elements ordinarily associated with sensory epithelium. There is no differentiation into sensory and supporting cells, sensory hairs are absent, and indeed specialized sensory cells seem to be altogether lacking. The nerve fibrils end freely on the lower surface of the cells of the deeper layer. The centrum has been regarded as the most important part of the ampulla, in which the nerves were supposed to end. As we have seen, this is not the case. The single layer of cubical cells covering the centrum cap seems to

furnish no support for the suggestion made by Fritsch ('90) that the centrum represents a sense organ which has lost its sensory function because of the pressure of the overlying mucus.

It therefore seems improbable that the ampullae serve as organs for the reception of stimuli which result in sensations of taste or audition, since the structures in vertebrates endowed with such functions have a characteristic epithelium consisting of supporting cells and sensory cells with sensory hairs. If the ampullae prove to have sensory function their structure (free nerve endings beneath an overlying epithelium) makes it more probable that they are of the nature of tactile sense organs.

Facts in support of the glandular theory are less easily attainable. The mucus is present in large quantities, it is true, filling ampullae and tubes; but I have never seen any indication of glandular activity in the cells, nor have any observations pointed to the fact that mucus is discharged from the cells. The very large size of the nucleus leaves little room in the cell for the processes of secretion, and the position of the nucleus at the peripheral end of the cell, where we should expect the mucus if made to be aggregated and discharged, is another fact opposed to the theory that we are dealing with a typical glandular structure.

An interesting correlation has been observed between the habits and the number of ampullae found in three of the selachians common at Woods Holl. As is well known, the shark is very active in its movements, the skate is less active, while the Torpedo is comparatively sluggish. The following table gives the result of a careful counting of the ampullae in the three forms above mentioned.

Number of ampullae in dogfish (*Galeus canis*) .	1595
Number of ampullae in skate (*Raja erinacea*) . .	779
Number of ampullae in Torpedo (*Torpedo occidentalis*)	220

In the structure of the individual ampullae one is struck with the complexity exhibited in Galeus, with the ten to twelve ampullary pockets, as compared with the relative simplicity of the six pockets of the Torpedo ampulla. In the skate the number of pockets is usually seven or eight.

In the lateral-line system of the same selachians there is a decreasing complexity observed in the animals less active in their habits. Galeus has a much-branched, dendritic system of tubules; in Raja the tubules are almost entirely simple, running in a direct course from the lateral-line canal to the surface pores; in Torpedo the same simple plan is observed on the dorsal surface, while on the ventral surface of the fish the lateral-line canal system has wholly disappeared, its place being taken, according to some writers (Garman, '88, Fritsch, '90), by Savi's vesicles.

Whether this simplicity of structure of lateral-line and ampullary organs is always correlated with sluggishness of habit is a question which can only be answered by a careful study of many different genera of the selachians.

Attention should be called, in the discussion of the glandular theory of the ampullae, to the fact that in Galeus, where the ampullae are most numerous, the skin is free from slime, while in the skate the slime is very abundant. It is highly improbable, therefore, that this slime is produced in the ampullae. On the other hand, an increase of sensory function would be expected to accompany a wider range of body movement.

Some experiments in cutting the nerves and studying the effect on the ampullae have been begun which may throw some light on the physiology of these organs. But at the present time no hypothesis yet suggested seems to me to explain the function of the ampullae in the economy of the life of the selachians.

My work on the ampullae of Lorenzini of the selachians was begun at the Marine Biological Laboratory at Woods Holl, Mass., in the summer of 1892. The original object of this research, as suggested by Dr. Howard Ayers, was to determine the relation (whether of contact or continuity) which exists between the nerve fibers and the cells of this so-called sense organ. The methylene blue stain seems to have given decisive evidence on that point. The problem has, however, gradually assumed a larger interest from the standpoint of comparative anatomy and physiology.

In conclusion I wish to express my appreciation of the help received from Dr. Howard Ayers and of the generous resources afforded me at the Williams College room in the Woods Holl Laboratories. A considerable portion of this investigation has been carried on at Harvard University and in the Williams College laboratories. I am especially indebted to Prof. E. L. Mark for his direction of my work during the year at Harvard; and to Dr. James I. Peck of Williams College for assistance in preparing my work for publication. The final copies of the drawings for this paper were made in ink by Dr. Arnold Graf.

MARINE BIOLOGICAL LABORATORY,
WOODS HOLL, MASS.
July 15, 1897.

LIST OF THE MORE IMPORTANT PAPERS ON THE AMPULLAE OF LORENZINI.

(*A complete bibliography of the subject will be given in a later paper.*)

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